Tree size, microhabitat, and hydraulic traits shape drought responses in a temperate broadleaf forest

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Summary

Predicting forest responses to drought is an increasingly critical task under climate change effects. Part of the problem is due to the lack of studies analyzing the confluence of leaf hydraulic traits with biophysical parameters. In this study, we analyze the interaction between these two trait groups using forest census data from a 25.6-ha ForestGEO plot in Virginia (USA). Drought periods were defined by both Palmer Drought Severity Indices (PDSI) and their identification from tree-ring records for 12 species representing 97% of woody productivity. Each drought scenario (1966, 1977, 1999), along with the overall trend, was then tested against leaf hyraulic trait measurements and microhabitat biophysical data. Individual-level growth responses to the three individual droughts were stronger in three cases: taller trees in dominant canopy positions, trees in wetter microsites, and more drought-sensitive species as assessed by leaf traits (turgor loss at less negative leaf water potential, greater shrinkage with leaf dehydration). However, there was substantial variation in the best predictor variables across given droughts. We conclude that when droughts occur, large dominant trees, drought-sensitive species, and individuals in wetter microhabitats are likely to be most strongly affected. **Add discussion points**

The Summary for research papers, which must be usable as a stand- alone document, must not exceed 200 words and should be organized using four bullet points to indicate: (1) the research conducted, including the rationale, (2) methods, (3) key results, and (4) the main conclusion, including the key points of discussion. It should not contain citations of other papers.

Introduction

Forests globally play a critical role in climate regulation (Bonan 2008), yet there remains enormous uncertainty as to how the terrestrial carbon (C) sink, which is dominated by forests, will respond to climate change (Friedlingstein et al. 2006). An important aspect of this uncertainty lies in responses to drought (**REF**). In many forested regions around the world, the risk of severe drought is increasing (Trenbert et al. 2014), even in conjunction with increasing precipitation (IPCC 2014). Global change-type drought has been affecting forests worldwide (Allen et al. 2015), and it is expected that future climate change-driven droughts will severely impact forests around the world (Allen et al. 2015; **REFS**). Larger trees tend to suffer more (e.g., (Bennett et al., 2015); Stovall et al. 2019), resulting in disproportionate impacts on forest C storage (Meakem et al. 2018). As a result, forest drought responses stand to strongly impact forest feedbacks to climate change (**REFS**), yet accurate characterization of drought responses remains a modeling challenge (**REFS**)– in part because some of the mechanisms underlying drought responses remain unclear. Understanding forest responses to drought requires increased functional understanding of how tree size, microhabitat, and species' traits jointly confer individual-level vulnerability or resistance, and the extent to which their influence is consistent across droughts.

One fundamental question regarding forest responses to drought is what drives the observed tendency for large trees to suffer more during drought. Bennett et al. (2015) showed that in forests globally, large trees suffer greater growth reductions during drought, and numerous subsequent studies have reinforced this finding (Stovall et al. 2019, **REFS**). However, this analysis quantified tree size based on DBH, which has no direct mechanistic meaning. This study proposed two major mechanisms–besides the tendency for bark beetles to preferentially attack larger trees (**REFS(KAT)**)–for the observed greater drought growth reductions of large trees. First, taller trees facea greater biophysical challenge of lifting water greater distances against the effects of gravity and friction (), and this may become a greater liability during drought

(**REFS(KAT)**). Second, larger trees may have lower drought resistance because they are more often in the canopy, where they are exposed to higher solar radiation, greater wind speeds, and lower humidity (**REFS(KAT)**). Alternatively, the generally supressed status of subcanopy trees may be insufficient to override the benefits of their buffered environment during drought. Potentially counteracting the biophysical challenges faced by large trees, their larger root systems may confer an advantage in terms of allowing greater access to water (**REFS(KAT)**); however, it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure. A final mechanism that could mediate tree size-related responses to drought is how hydraulic traits are distributed with respect to size (Meakem et al. 2018). It is possible that the pattern observed by Bennett et al. (2015) could be caused if the larger size classes were dominated by species less adapted to handle drought, be it through avoidance, resistance, or resiliance. Alternatively, larger size classes may be dominated by species that are better adapted to inherently greater biophysical challenges–as is the case in tropical moist forests of Panama, where larger size classes contain greater proportions of deciduous species (Condit et al. 2000; Meakem et al. 2018). Understanding the mechanisms underlying the tendency for larger trees to suffer more during drought will require sorting out the interactive effects of height, canopy position, root water acess, and species' traits.

A second fundamental question regarding forest responses to drought is how species' traits – alone and in interaction with tree size – influence drought response. To link drought responss to fundamental physiological characteristics, and because measuring and modeling drought responses of every species is infeasible in diverse forests, it is important to understand how traits shape drought responses. Commonly measured traits including wood density (WD) (**REFS**), leaf mass per area (LMA) (Abrams, 1990; Guerfel et al., 2009), and ring porosity (Elliot et al. 2015, Friedrichs et al. 2009) have been linked to drought responses in temperate deciduous forests–as well as in other forest biomes (**REFS**). However, these traits have less direct linkage to plant hydraulic function than leaf hydraulic traits such as leaf area shrinkage upon dessication (PLA_{dry}; **REF**) and turgor loss point (π_{tlp})–i.e., the water potential at which leaf wilting occurs (**REFS**), which are emerging as traits with potential to explain greater variation in plant distribution and function than the more commonly-measured traits such as WD and LMA (Medeiros et al. 2019). Their ability to predict tree performance under drought remains untested.

A final fundamental question regarding forest responses to drought is whether tree size and species' traits have similar influence across droughts, or whether drought variability in factors such as severity, duration, and timing interact with tree size and traits such that different components of the community respond differently to different droughts. No two droughts are the same, yet our ability to compare forest responses across droughts is hampered by the fact that droughts are rarely explicitly defined in ecological studies (Slette et al., 2019). Our knowledge of forest drought responses tends to come disproportionately from extreme droughts with dramatic impacts (*e.g.*, Allen et al. 2015; (Bennett et al., 2015); Stovall; **MORE REFS**), and our knowledge of forest responses to more modest but frequent droughts–e.g., those with historical return intervals on the order of a decade–remains more limited. While the tendency for larger trees to suffer more definitely predominates (Bennett et al., 2015), there are exceptions (e.g., **REFS**). There is also evidence that the degree to which larger trees suffer more increases with the severity of drought conditions ((Bennett et al., 2015); *Stovall et al. 2019 (I think!)*). [*Are there any studies showing interactions of drought type with traits?*] Thus, while we expect many of the fundamental mechanisms shaping drought responses to be universal, it is also likely that tree size and traits interact with drought characteristics to result in differential responses across droughts–but this has yet to be tested.

Here, we combine tree-ring records covering three droughts (1966, 1977, 1999), species functional and hydraulic trait measurments, and forest census data from a 25.6-ha ForestGEO plot in Virginia (USA) to test a series of hypotheses and associated specific predictions (Table 1) designed to yield functional understanding of how tree size, microenrivonment, and species' traits collectively shape drought responses. First, we focus on the role of tree size and its interaction with microenvironement. We confirm that, consistent with most forests globally, larger-diameter trees have lower drought resistance in this forest, which is in an ecoregion represented by only one study in (Bennett et al., 2015) (*H1.0*). We then test hypotheses designed to disentangle the relative importance of tree height (*H1.1*), crown exposure (*H1.2*), and root water access, which should be greater for larger trees in dry but not in perpetually wet microsites (*H1.3*). Second, we focus on the role of species' functional and hydraulic traits and their interaction with tree height. We hypothesize that drought resistance will follow predicted and observed patterns in relation to wood density, specific leaf area, and ring porosity , but that leaf hydraulic traits such as leaf area shrinkage upon dehydration and turgor loss point will prove better predictors (*H2.1*). We then test whether these traits correlate with tree height (*H2.2*), potentially driving the observed tendency for taller trees to suffer more during drought (*H2.3*). Finally, we focused on variability among droughts, asking how community resistance varied across droughts (*H3.1*) and whether the factors confirming vulnerability or resistance varied across droughts (*H3.2*).

Table 1. Summary of hypotheses, corresponding specific predictions, and results. We count predictions as fully supported / rejected when the response matches/contradicts the prediction in both univariate and multivariate models (when applicable). Parentheses indicate that predictions were partially supported/ rejected–i.e., that the direction of response matched/contradicted the prediction in some but not all models.

	Prediction supported?				
Hypotheses & Specific Predictions	Overall	1966	1977	1999	Results
H1.0. Larger-diameter trees have lower drought resistance.					
1.0- Drought resistance decreases with DBH.	yes	yes	(yes)	(no)	Table 4
H1.1. Drought resistance decreases with tree height.					
1.1a - Drought resistance decreases with height.	yes	yes	(yes)	(no/yes)	Tables 4, 5
1.1b - Height is a better predictor of drought resistance than DBH.	(yes)	(no)	(no)	-	Table 4
H1.2. Drought resistance decreases with crown exposure.					
1.2a - When CP is considered alone, dominant trees have lowest R.	(yes)	yes	(yes)	(no)	Table 4
1.2b - In models with CP and H, dominant trees have lowest R.	(no)	(no)	(yes)	(no)	Tables 4, 5
H1.3. Small trees (lower root volume) suffer more in drier microhabitats.					
1.3 - There is a negative interactive effect between H and TWI.	(no)	(no)	(no)	(no)	Table 4
H2.1. Species traits predict drought resistance.					
2.1a - WD correlates positively to drought resistant.	(no)	(no)	(no)	(yes)	Table 4
2.1b - LMA correlates positively to drought resistance.	(yes)	(yes)	(no)	(yes)	Table 4
2.1c - Diffuse porous species have lower drought resistance.	(yes)	(yes)	(no)	yes	Tables 4, 5
2.1d - PLA correlates negatively with drought resistance.	yes	yes	(yes)	(yes)	Tables 4, 5
2.1e - TLP correlates negatively with drought resistance.	(yes)	(yes/no)	(yes)	(yes)	Tables 4, 5
H2.2. Taller trees have more drought-resistant traits.					
2.1a - Community mean WD correlates positively to H.	no	-	-	-	Table S#
2.1b - Community mean LMA correlates positively to H.	yes	-	-	-	Table S#
2.1c - Community fraction of diffuse porous species decreases with H.	no	-	-	-	Table S#
2.1d - Community mean PLA correlates negatively to H.	no	-	-	-	Table S#
2.1e - Community mean TLP correlates negatively to H.	no	-	-	-	Table S#
H2.3. Size-dependent drought resistance is not driven by functional traits.					
2.3 - Effect of H is negative when traits are included in the statistical model.	yes	yes	(yes)	(yes)	Table 5
H3.1. Responses varied by drought.					
3.1 - Drought year explains variation in drought resistance.	no	-	-	-	Table 4
H3.2. Predictor variables varied across droughts.					
3.2a - Best predictor variables differ across droughts.	yes	-	-	-	Table 5
3.2b - Directions of responses to best predictor variables differ across droughts.	rarely	-	-	-	Tables 4,5

Materials and Methods

Study site

Research was conducted at the 25.6 ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W) (Bourg et al. 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level (Gonzalez-Akre et al., 2016) with a topographic relief of 65m (Bourg et al., 2013). Dominant tree taxa include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Data collection and preparation

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironemnt, and species traits (Table 2). The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems $\leq$ 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH, tree location in the plot to determine the topographic wetness index, and data for all stems $\geq$ 10cm to analyze functional trait composition relative to tree height (all analyses described below). Census data, which were last updated in 2018 (**confirm**), are available through the ForestGEO data portal.

Table 2. Summary of variables

variable	symbol	category	description	units	n	observed values median	min	max	ln-transformed?
Dependent variable									
drought resistance	R	-	ratio of growth during drought year to mean growth of the 5 years prior.	-	1596	0.87	0	1.99	no
Independent variables									
drought year	Y	1966		-	478	-	-	-	-
		1977		-	547	-	-	-	-
		1999		-	571	-	-	-	-
tree size:									
diameter breast height	DBH	-	DBH at time of drought	cm	all	31.92	3.92	134.19	yes
height	H	-	tree height at time of drought	m	all	20.21	4.76	43.87	yes
microhabitat:									
crown position	CP	dominant (D)		-	31	-	-	-	-
		co-dominant (C)		-	231	-	-	-	-
		intermediate (I)		-	224	-	-	-	-
		suppressed (S)		-	101	-	-	-	-
topographic wetness index	TWI	-		-	all	5.66	0	16	yes
species' traits:									
wood density	WD	-	dry mass of a unit volume of fresh wood	g cm-3	all	0.62	0.4	1.09	no
leaf mass per area	LMA	-	ratio of leaf dry mass to fresh leaf area	kg m-2	all	48.69	30.68	75.8	no
ring porosity	RP	ring		-	408	-			-
		semi-ring		-	31	-			-
		diffuse		-	178	-			-
turgor loss point	TLP	-		MPa	all	-2.39	-2.76	-1.92	no
percent loss area	PLA	-	percent loss of leaf area upon dessication	%	all	13.06	8.52	24.64	no

We analyzed tree-ring data from 571 trees representing the twelve species contributing most to woody aboveground net primary productivity (ANPP), which together comprised 97% of study plot ANPP between 2008 and 2013 (Helcoski et al., 2019). Cores were obtained in 2010-2011 or 2016-2017 from a breast height of 1.3m using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals of DBH $\geq$ 10cm (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with Helcoski et al. (2019): (ITRDB; GitHub/Zenodo). *Ryan submitted the data to ITRDB but I don't think its posted yet. We should also cite GitHub/Zenodo here. I'll come back to that.*

For each tree, we combined tree-ring records and allometric equations of bark thickness to retroactively calculate DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[\sum_{year=Y}^{2008} (r_{ring,Y} : r_{ring,2008}) - r_{bark,Y} + r_{bark,2008}\right]$$

Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to DBH (Table S#) and then used these to estimate bark thickness based on DBH.

Height measurements (n=# trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository. Measurement methods included manual (Stovall et al., 2018a, NEON), digital rangefinders (Anderson-Teixeira et al., 2015b), and automatic LiDAR (Stovall et al., 2018b). Rangefinders either used the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013). Species-specific height allometries were developed (Table S#). For species with insufficient height data to create reliable species-specific allometries, heights were calculated from equations derived from all species in the study.

Crown positions were recorded in the field during the growing season of 2018 following the crown position protocol from (Jennings et al., 1999), whereby positions were ranked as dominant, codominant, intermediate, or suppressed. As there was no way to retroactively estimate crown position, we assumed that 2018 crown position was reflective of each tree's position over the past 60 years. While some trees undoubtedly changed position, an analysis of crown position relative to height (Fig. 2) and height change since *1959* indicated that change was likely slow. Specifically, [**Ian, please provide details–e.g., average rate of height growth**]

Topographic wetness index (TWI) was calculated using the (**?**) package in R. [** Ian, include a brief explanation of what this is**]

Hydraulic traits were collected from SCBI and are summarized in Table 3. In August 2018, we sampled small sun-exposed branches from three individuals of each species in and around the ForestGEO plot. These were covered with opaque plastic bags, re-cut under water, and re-hydrated overnight before further analysis. Rehydrated leaves (n=3 per indivdiual) were scanned, weighed, dried at 60° C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using an R script (**details**). LMA was calculated as the ratio of leaf dry mass to fresh area. PLA was calculated as the percent loss of area between fresh and dry leaves. WD was calculated for ~1cm diameter stem samples (bark and pith removed) as the ratio of dry weight to volume. We used the rapid determination method of ([Bartlett et al., 2012]) to estimate the turgor loss point (π_{tlp}). Briefly, two 4mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ ([Bartlett et al., 2012]). We also characterized hydraulic vulnerability curves for the # most productive species, but because P50 and P80 [**define**] did not come out as top predictors in preliminary analyses and their inclusion limited the set of species that could be included in the full analysis, these traits were dropped from further consideration. Data and R scripts for hydraulic traits are available at [**create new public GitHub repo for hydraulic traits, archive in Zenodo, give DOI**].

(**add description of climate data used in Fig. 1, NEON vertical profiles**)

Identification of drought years

We identified droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events where tree growth was substantially reduced and where peak growing season climatic conditions were among the driest of the time period. To identify years with widespread reductions in tree growth, we used the pointRes package (**?**) in R (version 3.5.3) to determine drought periods based on trees' drought resistance, which is defined as the ratio between the performance during and before the disturbance (Lloret et al., 2011). Specifically, we looked at the ratio between annual basal area increment (BAI) in the year of the drought to average annual BAI in the 5 preceding years. Candidate drought years were defined if >25% of the cored trees experienced <30% growth in a year compared to the previous 5 years. Separately, we identified the years with driest conditions during May-August, which stood out in the analysis of (Helcoski et al., 2019) as the months (of the current year) to which annual growth was most sensitive for trees at this site. We considered two metrics of moisture deficit: regional Palmer Drought Severity Index (PDSI) values [**source-**

Table 3. Overview of analyzed species, their productivity in the plot, numbers and sizes sampled, and traits. Given are DBH mean and range of cored trees, the number of cores represented by each crown position of each species, and mean hydraulic trait measurements. Units of measurements are in mm (DBH), % (PLA), g/m2 (LMA), MPa (TLP), and g/cm3 (WD).

sp	mean_DBH	range_DBH	RP	PLA	LMA	TLP	WD
caco	271.87	508.0	ring	17.22	45.86	-2.13	0.83
cagl	313.89	887.0	ring	21.09	42.76	-2.13	0.62
caovl	352.87	511.0	ring	14.80	47.60	-2.48	0.96
cato	209.74	201.1	ring	16.56	45.36	-2.20	0.83
fagr	235.11	960.0	diffuse	9.45	30.68	-2.57	0.62
fram	353.63	883.3	ring	13.06	43.28	-2.10	0.56
juni	481.42	628.0	semi-ring	24.64	72.13	-2.76	1.09
litu	368.54	904.0	diffuse	19.56	46.92	-1.92	0.40
qual	471.51	677.0	ring	8.52	75.80	-2.58	0.61
qupr	422.48	767.0	ring	11.75	71.77	-2.36	0.61
quru	548.79	1369.3	ring	11.01	71.13	-2.64	0.62
quve	541.38	981.8	ring	13.42	48.69	-2.39	0.65

NOAA-same as Helcoski] and the difference between potential evapotranspiration (PET) and precipitation (PRE) [**source- same as Helcoski**]. The driest years were identified through simply ranking mean May-August PDSI or [PET-PRE] for the time period from driest to wettest.

Analysis (**this needs work**)

Linear mixed models were run following the order of the hypotheses as seen in Figure ??? [individual_tested_traits]. Using the (**?**) package, we set up models with the resistance value as the response variable (excluding outliers with values of $R \geq 2$), and each prediction's variable as the independent variable. Variables' importance in predicting drought tolerance was calculated from mixed-effects models and the lowest AICc (**?**, **?**).Null models were determined in order of the predictions. First, we analyzed the combined scenario to determine if "year" was significant. Upon establishing this, we tested height and DBH as size parameters. Although both were significant, height was kept due to its larger delta AICc compared with the null model. We then tested the remaining biophysical and hydraulic traits individually against a null model containing height and year. This yielded Figure ??? (cand_full). All variables with dAICc >2 were used as candidates for each scenario's best model (figure ???? (tested_traits_best))

Results

Descriptions of Droughts

In the 60-year period between 1950 and 2009, there were three droughts that met our criteria of anomalously dry climatic conditions coupled with substantial reductions in tree growth for at least some portions of the community: 1966, 1977, and 1999 (Fig. 1). We excluded one year (1991) meeting the growth reduction criteria (26.5% of trees experienced >30% growth reduction, mean resistance= -13.8%) because this year was not among the strongest droughts of the study period (**DETAILS**). Rather, the severity of growth reduction may be explained by defoliation by gypsy moths (*Lymantria dispar* L.) from approximately 1988-1995, which most stronly impacted *Quercus* spp. (**Cite Shenanadoah paper, if accepted**). Climatically, these droughts included three of the five years between 1950 and 2009 with greatest moisture deficit (PET-PRE) during the peak growing season months of May-August, which are the months to which annual tree growth at this site is most sensitive (Helcoski et al., 2019). Specifically, 1966, 1977, and 1999 had mean MJJA PET-PRE of 83.37, 86.97, and 80 mm mo-1, respectively. The years 1964 and 2007 also ranked in the top five driest (PET-PRE =83.87 and 82.13 mm mo-1), but *were not among the lowest in terms of PDSI and were not identified as a pointer yeasr.* **The droughts differed in timing/duration/etc. .. The year 1966 was preceded by two relatively dry years... 1964 among five driest in terms of May-August [PET-PRE], 1965 also anomalously hot and dry.**

Community-level tree growth responses to these droughts were modest, with modal resistance values of #, #, and # for 1966, 1977, and 1999, respectively (Fig. 1b). In each drought, roughly 30% of the cored trees suffered growth reductions of 30% or more (resistance <= 0.7): #% in 1966, #2% un 1977, and #% in 1999. *Some* trees exhibited increased growth: (resistance > 1.0): #% in 1964-66, #% un 1977, and #% in 1999. Within the context of mixed effects models, there were no significant differences in resistance across drought years (Table 4).

			all droughts		1966		1977		1999	
variable	**category**	**null variables**	**dAICc**	**coefficients**	**dAICc**	**coefficients**	**dAICc**	**coefficients**	**dAICc**	**coefficients**
drought year	1966		-2.42	0						
	1977			-0.0209						
	1999			-0.0105						
ln[DBH]		Y	**8.17**	-0.0385	**15.32**	-0.0888	-0.87	-0.0214	-1.93	0.0057
ln[height]		Y	**8.80**	-0.0648	**15.27**	-0.1443	-0.98	-0.0335	-2.03	0.0018
crown position	D	Y	-2.96	-0.0461	**3.25**	-0.0509	0.66	-0.0759	0.38	-0.0103
(alone)	C			0		0		0		0
	I			-0.0063		0.0732		-0.0298		-0.0563
	S			0.0122		0.0526		0.0432		-0.0483
crown position	D	ln[H]+Y	0.55	-0.0364	-1.41	-0.0359	-0.24	-0.074	**3.99**	-0.0027
(with height)	C			0		0		0		0
	I			-0.0406		0.0177		-0.0363		-0.0823
	S			-0.0586		-0.0654		0.03		-0.1011
ln[TWI]		ln[H]+Y	**5.33**	-0.0886	-1.96	-0.0168	**5.06**	-0.1406	**2.72**	-0.1025
ln[height]*ln[TWI]		ln[H]+ln[T]+Y	-1.18	0.0677	-1.75	0.0749	-1.86	0.0533	-1.79	0.0566
wood density		ln[H]+Y	-1.89	-0.0498	-1.10	-0.2161	-1.19	-0.1827	0.23	0.2512
leaf mass per area		ln[H]+Y	-2.00	0.0003	-1.89	0.0011	-1.74	-0.0014	-1.99	0.0005
ring porosity	ring	ln[H]+Y	-2.40	0.0574	1.78	0.151	0.59	-0.1879	**4.25**	0.2025
	semi-ring			-0.0335		-0.1324		-0.1426		0.1516
	diffuse			0		0		0		0
turgor loss point		ln[H]+Y	1.22	-0.1675	-1.78	-0.0845	1.14	-0.2432	0.06	-0.1749
percent loss area		ln[H]+Y	**7.89**	-0.0138	**9.82**	-0.0244	-0.07	-0.0104	-0.73	-0.0074

#this is tested_traits_all

Results for first main question: what drives the observed tendency for large trees to suffer more during drought? H1.0, H1.1, H1.2, H1.3 DBH, height, crown position, and TWI

Results for second main question: how do species' traits - alone and in interaction with tree size - influence drought response? H2.1, H2.2, H2.3 Hydraulic traits alone, traits with height

Results for third main question: are responses similar or variable across individual drought

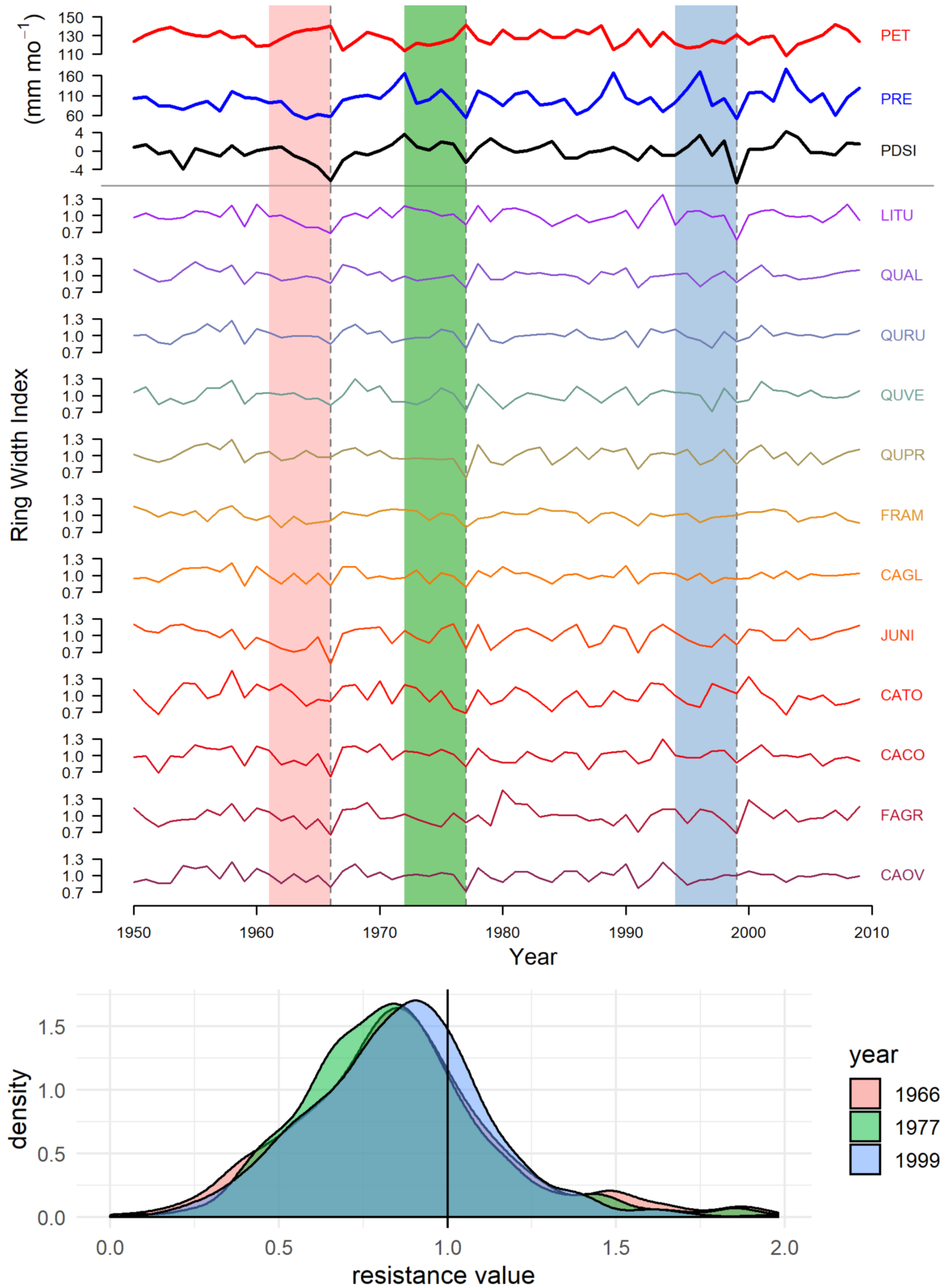
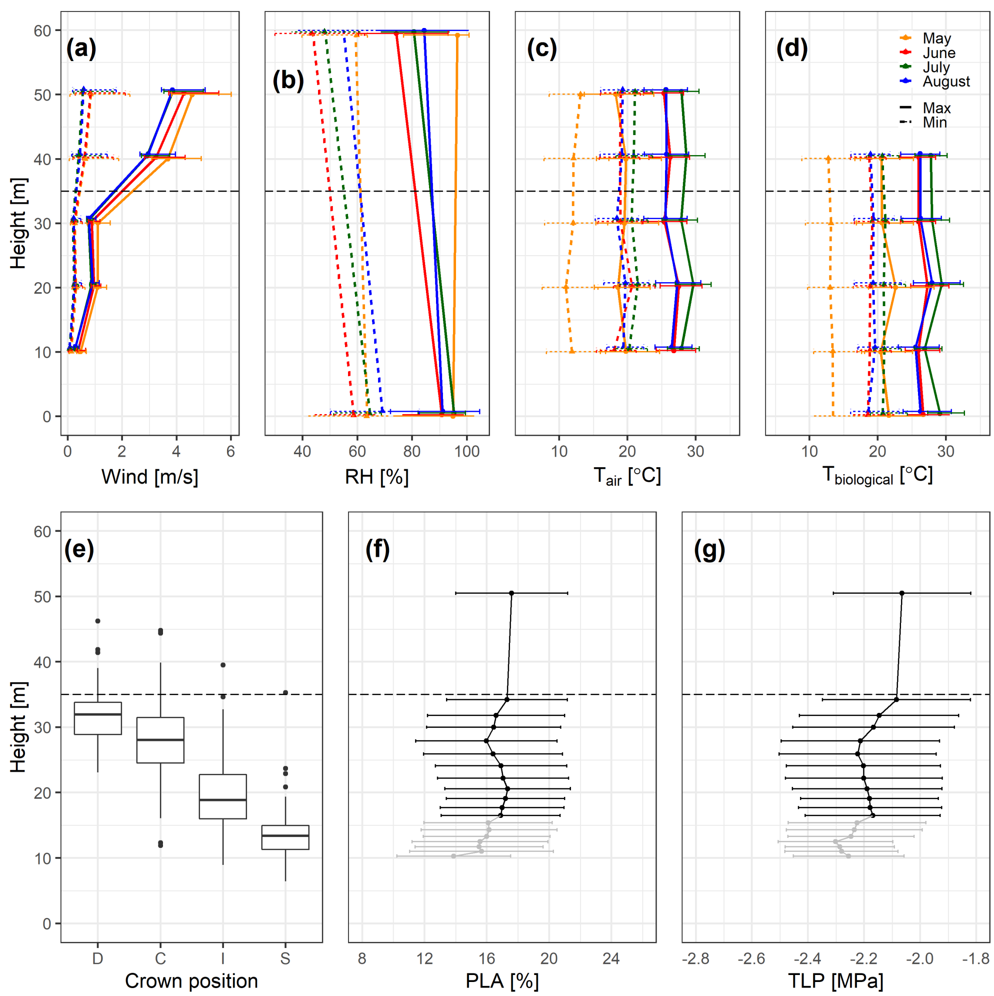


Figure 1. (a) Time series of peak growing season (May-August) climate conditions and residual chronologies for each species. Droughts analyzed here are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski et al., 2019). (b) density plots of community-wide resitance values for each drought.

					Canopy position					ring porosity				
drought	dAICc	R^2	Intercept	ln[H]	D	C	I	S	ln[TWI]	diffuse	semi-ring	ring	PLA	TLP
all	0	0.11	1.108	-0.062	-	-	-	-	-0.085	-	-	-	-0.012	-0.105
	0.338	0.1	1.494	-0.097	-0.036	0	-0.038	-0.056	-0.078	-	-	-	-0.013	-
	0.403	0.12	1.263	-0.096	-0.035	0	-0.036	-0.053	-0.078	-	-	-	-0.012	-0.087
	0.515	0.12	1.393	-0.064	-	-	-	-	-0.087	0	0.147	0.048	-0.017	-
	0.571	0.1	1.375	-0.061	-	-	-	-	-0.085	-	-	-	-0.013	-
	0.903	0.12	1.492	-0.098	-0.034	0	-0.036	-0.053	-0.079	0	0.122	0.049	-0.016	-
1996	0	0.26	2.271	-0.153	-	-	-	-	-	0	0.35	0.152	-0.035	0.25
	0.537	0.26	1.537	-0.154	-	-	-	-	-	0	0.098	0.133	-0.023	-
	1.093	0.27	2.389	-0.177	-0.038	0	0.016	-0.068	-	0	0.352	0.153	-0.035	0.27
	1.434	0.24	1.629	-0.143	-	-	-	-	-	-	-	-	-0.024	-
	1.982	0.26	2.307	-0.152	-	-	-	-	-0.016	0	0.356	0.152	-0.035	0.254
1977	0	0.22	0.346	-	-0.074	0	-0.027	0.042	-0.131	0	-0.331	-0.23	-	-0.384
	0.09	0.21	0.393	-	-	-	-	-	-0.14	0	-0.324	-0.23	-	-0.369
	1.116	0.21	0.46	-0.026	-	-	-	-	-0.137	0	-0.316	-0.23	-	-0.367
	1.914	0.22	0.367	-0.006	-0.073	0	-0.029	0.037	-0.13	0	-0.33	-0.23	-	-0.383
1999	0	0.25	1.284	-0.081	0.003	0	-0.077	-0.095	-0.087	0	0.22	0.193	-0.008	-
	0.085	0.25	0.844	-0.082	0.001	0	-0.078	-0.095	-0.085	0	0.062	0.185	-	-0.142
	0.462	0.23	1.174	-0.083	0.002	0	-0.079	-0.099	-0.088	0	0.135	0.2	-	-
	0.956	0.24	1.042	-	-	-	-	-	-0.1	0	0.261	0.191	-0.01	-
	1.029	0.24	0.7	-0.09	-0.002	0	-0.082	-0.101	-	0	0.046	0.185	-	-0.151
	1.193	0.24	1.159	-0.089	0	0	-0.081	-0.101	-	0	0.21	0.194	-0.008	-
	1.326	0.24	0.533	-	-	-	-	-	-0.098	0	0.077	0.181	-	-0.161
	1.849	0.26	1.046	-0.079	0.002	0	-0.077	-0.094	-0.086	0	0.14	0.188	-0.005	-0.078
	1.851	0.22	1.045	-0.092	-0.001	0	-0.084	-0.105	-	0	0.123	0.201	-	-

Table 5 - best full models

years? H3.1 and H3.2 Combining biophysical with hydraulic traits, which come out as candidates for best model?



Height profile graphs

Discussion

Discussion outline

- first paragraph is summary of main findings, not re-presenting the results
- "we supported this hypothesis, but not this one" (following same order as Table 1 still)
- direction of responses seems to be relatively consistent but the individual responses vary
- tie things in (see here
- main thing is that we're now better understanding what confers vulnerability or resilience on trees during drought - how forests respond to future droughts/climate change
- "we filled the gap" = 1-2 sentences
- limitations at our site:
- aren't able to analyze historical forest community, nor trees that were killed by these droughts [aka we don't have data for individuals that were most severely affected] (though we found that there's little variation in climate sensitivity for trees that were cored dead vs cored alive).
- p50/p80
- We used crown position despite its uncertainty. However, height and crown position change relatively slowly so it shouldn't be that far off.
- We did not use crowding index because it has much more uncertainty
- limitations for extrapolating other sites:
- forests are different from place to place, but we've seen how in forests around the world, forests tend to suffer more. We've identified some facets for why this happens. (cite other studies)
- has been observed elsewhere that individuals in more moist habitats are more susceptible to drought (cite other studies)
- the species may be different from other sites but the hydraulic traits are general across species;
- next paragraph saying that our study advances understanding of droughts, e.g. bennett et al 2015 doesn't go into mechanisms but we do
- and we show that height is more important than exposure, but doesn't eliminate the effect of it
- further contribution is we show that two leaf hydraulic traits - relatively easy to measure - are good predictors of drought response, can be helpful for scaling up (e.g. from our site to eastern deciduous biome)
- biophysical mechanisms are things that should be seen as universal but relative importance of each can vary within each drought
- first study to show how these traits affect woody growth response to drought **confirmed by Lawren**
- science is better now. by advancing our understanding of the mechanisms for individual-level responses to drought, this opens door for better predictions (elaborate from above). "This is absolutely critical to predicting forest responses to future droughts, which we're likely to see more of in the future as a result to climate change. Forecasting forest responses to these droughts is a huge and important challenge", science is better.

1. paragraph summarizing main results–> primary conclusions When including only biophysical traits, trees' resistance value (on a per-species basis) is explained best by crown position and height, with codominant trees being the most resistant to drought. This follows on work done by (Bennett et al., 2015) [and others?] which show that larger trees suffer more during drought, and confirms that this susceptibility can be seen in tree ring analyses. Adding in crown position with the leaf hydraulic traits yields a slightly worse predictive model for drought tolerance, with height remaining as the only significant biophysical variable.

We partially supported the hypothesis that crown exposure makes trees more vulnerable to drought. Co-dominant trees had the highest drought resistance. Dominant trees had lower resistance, likely because they are the most exposed. Other studies have found clear evidence of greater drought sensitivity in trees with exposed crowns (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)). At the same time, intermediate and suppressed trees had even lower resistance. This indicates that other mechanisms such as competition or rooting depth were important. (Also note that our study design was not ideal for testing the role of canopy position. Current canopy position is a conservative separator of canopy position: trees may currently be in more dominant positions than they were at the time, but backwards movement is unlikely. This would bias against finding a signficant effect for H1.2. Height may be a more reliable predictor of past canopy position than is current canopy position, and explains a portion of variation in canopy position.)

Proximity to stream–either vertical (elev) or horizontal (distance)– did not increase drought resistance; rather, it tended to decrease resistance (H1.3a). This may be because individuals growing further from water are acclimatized to drier conditions. However, the increase in drought resistance with distance from stream was less for small than large trees (H1.3b), indicating a potential importance of root depth/volume in conferring drought resistance.

misc content to integrate From (Kannenberg et al., 2019), species with diffuse porous wood anatomy (*Liriodendron*) are more sensitive to drought, whereas ring-porous are not as affected because they more easily rebuild structures for hydraulic conductivity. This paper mentions it would be good to have this data with respect to latent affects from drought.

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Author Contribution

words

Supplementary Information

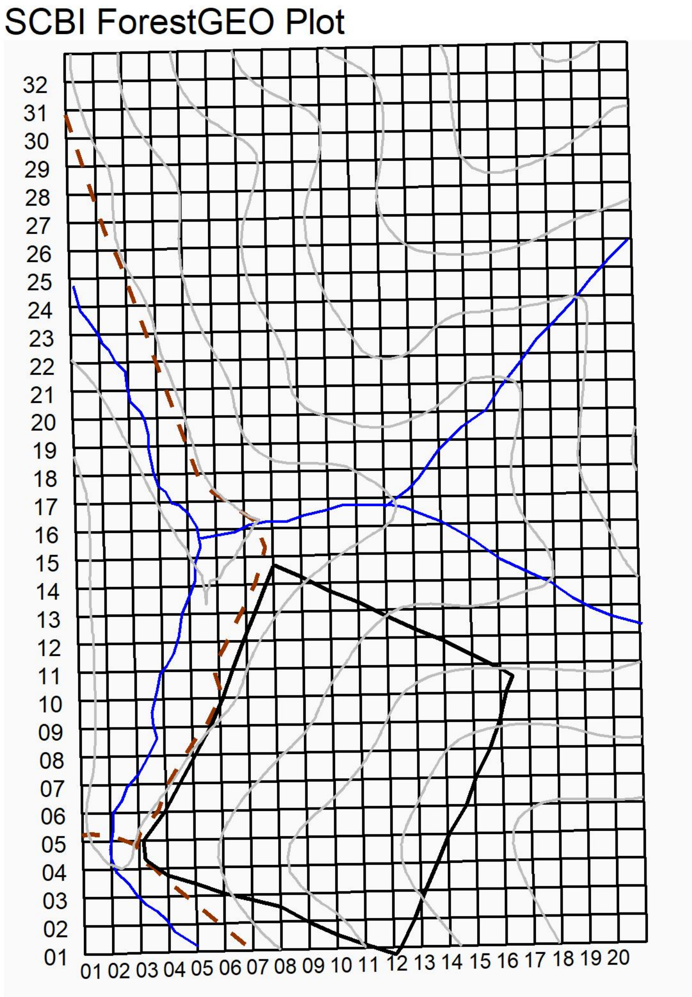
Species-specific height regression equations

Species	Equations	r.2
Carya cordiformis	0.348+0.808*x	0.879
Carya glabra	0.681+0.704*x	0.855
Carya ovalis	0.621+0.722*x	0.916
Carya tomentosa	0.776+0.701*x	0.894
Fagus grandifolia	0.708+0.662*x	0.857
Liriodendron tulipifera	1.32+0.524*x	0.761
Quercus alba	1.14+0.548*x	0.647
Quercus prinus	0.44+0.751*x	0.869
Quercus rubra	1.17+0.533*x	0.773
all	0.879+0.634*x	0.857

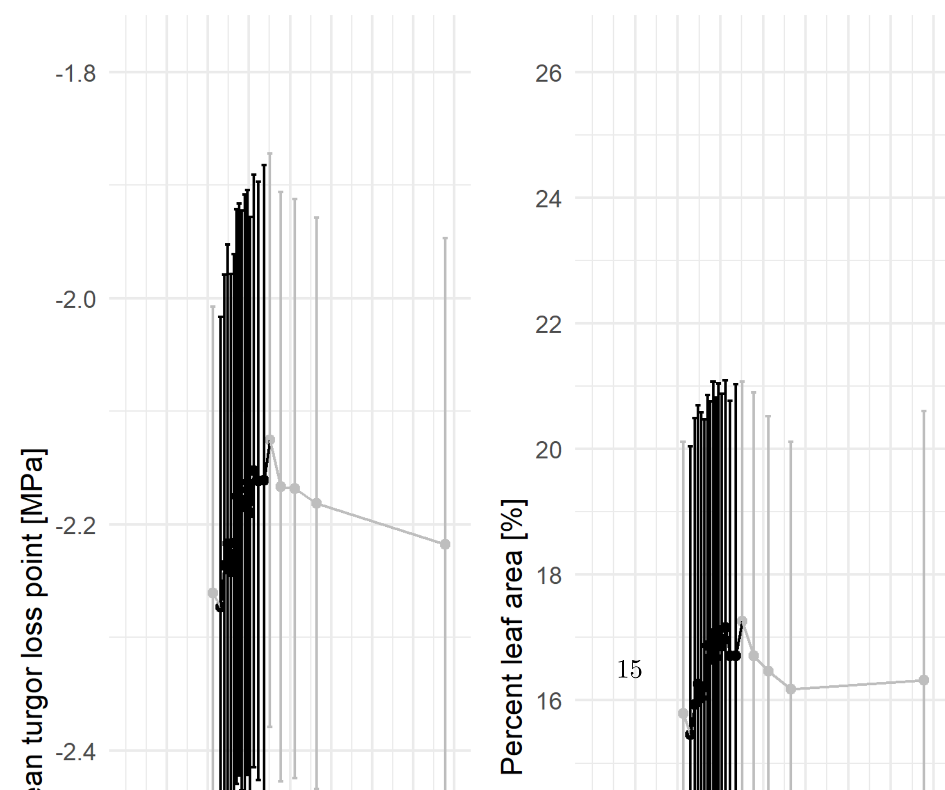
Candidate variables for best model

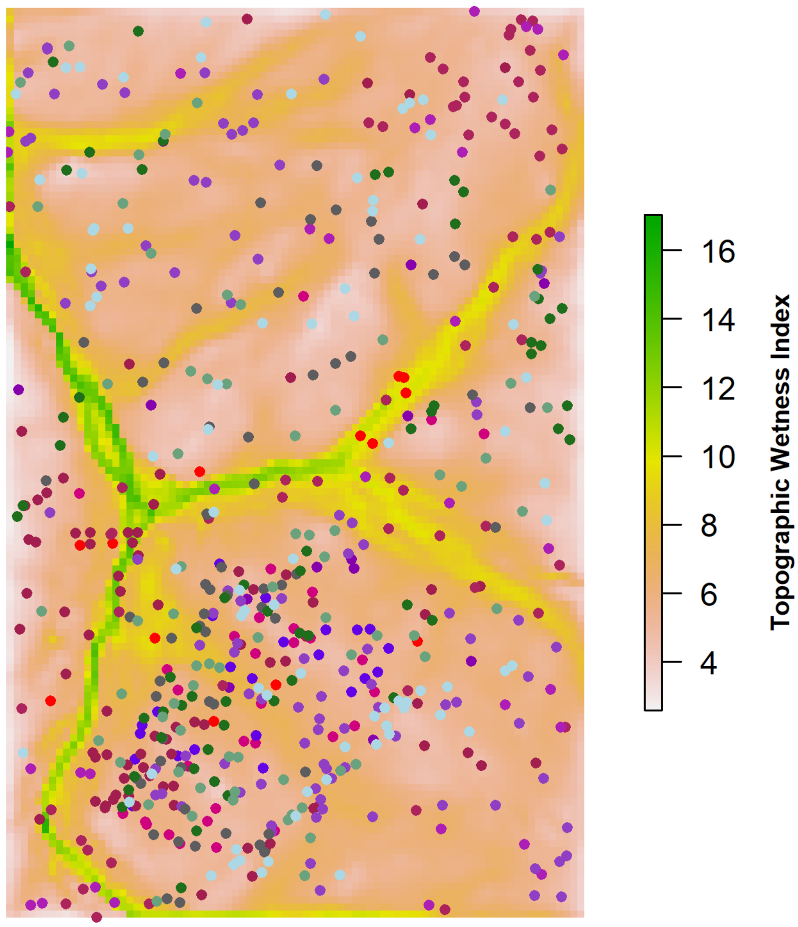
prediction	variable	variable_description	top_model
1.2	position_all	crown.position w/height	1999
2.2	height.ln.m	ln[height]	all
2.2	height.ln.m	ln[height]	1966
2.3	position_all	crown.position alone	1966
2.4	TWI.ln	ln[topographic.wetness.index]	all
2.4	TWI.ln	ln[topographic.wetness.index]	1977
2.4	TWI.ln	ln[topographic.wetness.index]	1999
3.1	rp	ring.porosity	1966
3.1	rp	ring.porosity	1999
3.2	PLA_dry_percent	percent.loss.area	all
3.2	PLA_dry_percent	percent.loss.area	1966
3.4	mean_TLP_Mpa	mean.turgor.loss.point	all
3.4	mean_TLP_Mpa	mean.turgor.loss.point	1977

how do we want to present Table S3? Would it be better as an image of an excel file, since it's so large? Did we want to keep all coefficients here?



Map of ForestGEO plot





Location of cored trees

Top model variations for each drought scenario, with dAICc values <= 2

Modnames	Delta_AICc	scen
resist.value ~ height.ln.m+TWI.ln+PLA_dry_percent+mean_TLP_Mpa+(1|sp/tree)	0.00	trees
resist.value ~ position_all+height.ln.m+TWI.ln+PLA_dry_percent+(1|sp/tree)	0.34	trees
resist.value ~ position_all+height.ln.m+TWI.ln+PLA_dry_percent+mean_TLP_Mpa+(1|sp/tree)	0.40	trees
resist.value ~ height.ln.m+TWI.ln+rp+PLA_dry_percent+(1|sp/tree)	0.52	trees
resist.value ~ height.ln.m+TWI.ln+PLA_dry_percent+(1|sp/tree)	0.57	trees
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+(1|sp/tree)	0.90	trees
resist.value ~ height.ln.m+rp+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	0.00	x196
resist.value ~ height.ln.m+rp+PLA_dry_percent+(1|sp)	0.54	x196
resist.value ~ position_all+height.ln.m+rp+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	1.09	x196
resist.value ~ height.ln.m+PLA_dry_percent+(1|sp)	1.43	x196
resist.value ~ height.ln.m+TWI.ln+rp+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	1.98	x196
resist.value ~ position_all+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.00	x197
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.09	x197
resist.value ~ height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	1.12	x197
resist.value ~ position_all+height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	1.91	x197
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+(1|sp)	0.00	x199
resist.value ~ position_all+height.ln.m+TWI.ln+rp+mean_TLP_Mpa+(1|sp)	0.09	x199
resist.value ~ position_all+height.ln.m+TWI.ln+rp+(1|sp)	0.46	x199
resist.value ~ TWI.ln+rp+PLA_dry_percent+(1|sp)	0.96	x199
resist.value ~ position_all+height.ln.m+rp+mean_TLP_Mpa+(1|sp)	1.03	x199
resist.value ~ position_all+height.ln.m+rp+PLA_dry_percent+(1|sp)	1.19	x199
resist.value ~ TWI.ln+rp+mean_TLP_Mpa+(1|sp)	1.33	x199
resist.value ~ position_all+height.ln.m+TWI.ln+rp+PLA_dry_percent+mean_TLP_Mpa+(1|sp)	1.85	x199
resist.value ~ position_all+height.ln.m+rp+(1|sp)	1.85	x199

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